University of Alberta

Compensatory Water Relations in Aspen Following Defoliation

by

Miranda M. Hart

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

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Abstract

Defoliation by forest tent caterpillars (*Malacosoma disstria* Hübner) is widespread in aspen (*Populus tremuloides* Michx.). Stomatal conductance, leaf water potential, and sap flow of aspen were measured in response to defoliation. In the field, there was evidence of increased stomatal conductance in trees with 50% and 98% defoliation, but no change in leaf water potential. Sap flow, however, decreased in trees with 98% defoliation. Under controlled conditions, stomatal conductance and rate of photosynthesis were measured under high and low vapour pressure deficits (VPD). Under high VPD, overall stomatal conductance and rates of photosynthesis were reduced. However, in both VPD treatments, there was increased stomatal conductance and compensatory photosynthesis following defoliation. These may relate to increases in leaf specific hydraulic conductance following defoliation. The results suggest that while the observed compensation was insufficient to compensate for loss of leaf area in severely defoliated trees, moderate defoliation may have little impact on growth in aspen.

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List of Symbols

E.....evoaptranspiration (mmol m^{-2} s^{-1})

E_{leaf}.....leaf specific evapotranspiration

g_s.....stomatal conductance (mmol m^{-2} s^{-1})

K.....hydraulic conductance

K_{leaf}.....leaf specific hydraulic conductance

ψ_{leaf}.....leaf water potential (MPa)

VPD.....vapour pressure deficit (kPa)

S_T.....tree-level sap flow (cm/s)

Introduction

Aspen and Forest Tent Caterpillars

Trembling aspen (*Populus tremuloides* Michx.) is the most widespread tree species in North America (Schier 1975). It is a dominant species in the boreal forest and aspen parkland, and is the only naturally occurring tree in prairie ecosystems (Peterson and Peterson 1992). In the last 20 years, aspen has become a valuable commodity, with the development of pulp and oriented strand board technologies (Darran 1991, Gower *et al.* 1996). It is particularly significant to the forest industries in the prairie provinces, where it makes up a considerable portion of forest revenues (Anonymous 1997).

Defoliation by forest tent caterpillars (*Malacosoma disstria* Hübner) is the most significant stress on aspen stands (Ives and Wong 1988). Major infestations occur approximately every ten years and may last as long as five years (Peterson and Peterson 1992). During an infestation, entire stands can be completely defoliated (Ives and Wong 1988).

The consequences of defoliation can be serious if defoliation is extreme and occurs for more than one season. In conjunction with drought, severe defoliation can cause stand-level dieback of aspen (Schoenweiss 1975, Hogg and Hurdle 1995). It is thought the massive dieback of aspen stands throughout the aspen parkland is due to the combination of successive years of drought and defoliation (Zoltai *et al.* 1991, Hogg and Schwarz 1997). Stands that are not killed outright by defoliation are highly vulnerable to pathogens which contribute to stand dieback (Zoltai *et al.* 1991).

Compensatory Photosynthesis

Despite the importance of aspen and the severity of defoliation stress, there has been little research into recovery mechanisms in aspen following defoliation. Production of unpalatable or lethal toxins is one strategy some plants use to prevent herbivory. A study examining the chemical response following defoliation found that aspen produces tannins and phenolic glycosides which are toxic to herbivores (Lindroth and Bloomer 1991).

A more significant response might be the enhanced $C0_2$ assimilation in residual leaves after defoliation (Hoogesteger and Karlsson 1992). The phenomenon, compensatory photosynthesis, describes the increase in the rate of photosynthesis of foliage on a partially defoliated plant relative to foliage of the same age on an undefoliated plant (Nowak and Caldwell 1984). This topic has been covered extensively, and many studies have shown that plants can partially compensate for lost leaf area by increased CO_2 assimilation rates at leaf level (Hodgkinson 1974, Alderfer and Eagles 1976, Detling *et al.* 1979, Wallace *et al.* 1984, Heichel and Turner 1983, von Caemmerer and Farquhar 1984, Ovsaka *et al.* 1992, Peterson *et al.* 1992, Meinzer and Grantz 1990, Hoogesteger and Karlsson 1992, Meinzer *et al.* 1992, Morrison and Reekie 1995). To the best of my knowledge, there are no studies examining the response of aspen to defoliation.

Improved resource status

While there is agreement that compensatory photosynthesis sometimes occurs following defoliation, there is little consensus as to how it happens. The earliest studies

approached it from a resource partitioning perspective (Alderfer and Eagles 1976, Layne and Flore 1993). From this perspective, defoliation reduces competition between leaves for resources (Ovsaka *et al.* 1992). Residual leaves have more light, nutrients and water and thus can immediately increase photosynthesis rates (McNaughton 1983), and perhaps benefit from longer leaf activity by delaying leaf senescence (Hodgkinson 1974, Nowak and Caldwell 1984).

Improved water status

While nutrient status is ameliorated by defoliation, this approach is inconclusive because it fails to consider the parallel increase in stomatal conductance that accompanies an increase in assimilation (McNaughton 1983, Nowak and Caldwell 1984, Wallace *et al.* 1984, Gold and Caldwell 1989, Meinzer and Grantz 1990, Hoogesteger and Karlsson 1992, Peterson *et al.* 1992, Heichel and Turner 1983, Ovsaka *et al.* 1993, Paez and Gonzalez 1995, Morrison and Reekie 1995). Improved water relations may be the most significant aspect of compensatory photosynthesis (McNaughton 1983). A more comprehensive understanding of compensatory photosynthesis requires an examination of the role of water in a plant from the soil to the atmosphere.

Plant water relations

The challenge facing all plants is the same: how to maximize $C0_2$ uptake while minimizing water loss? Stomatal regulation is central to this problem; guard cells allow the $C0_2$ in, while letting the water vapour out. How stomates respond to water stress has been under recent scrutiny (Collatz *et al.* 1991, Mott and Parkhurst 1991, Monteith 1995,

Franks *et al.* 1997). To understand how water relations might contribute to compensatory photosynthesis, it is essential to consider the path of water as it moves from the soil into the roots, up the stem, and into the leaves, where it exits as vapour.

Transpiration (E) pulls water up, from the soil to the leaves (Tyree and Sperry 1988). The resulting tension in the water column (water potential, ψ) is weakest in the roots. Up the tree, tension increases, and ψ becomes more negative. Tension is further increased as soil moisture decreases, or E increases. The maximum rate of E is determined by the hydraulic conductance of the tree (K), which is the capacity of the roots and stem to supply leaves with water (Meinzer *et al.* 1992). As resistance to water flow increases (by low ψ_{soil} or xylem embolism), tension increases causing a steeper ψ gradient (Sperry *et al.* 1993). If the gradient becomes too steep, low ψ_{leaf} may incite xylem cavitation. In some cases this can develop into catastrophic xylem embolism - the ψ_{leaf} continues to drop to maintain water movement up the tree, but instead incites massive xylem cavitation (Tyree and Sperry 1988). However, this does not normally occur. Instead, stomates close, limiting E and maintaining ψ_{leaf}, before the threshold for catastrophic xylem embolism is reached (Tyree and Sperry 1988, Sperry and Pockman 1993, Sperry *et al.* 1993). In general, plants are thought to function around the threshold ψ_{leaf} for cavitation, to maximize E, and thus photosynthesis (Sperry and Pockman 1993).

Vapour pressure deficit (VPD) is the difference between the vapour pressures of ambient and saturated air at leaf temperature (Larcher 1980) and represents plant water status at the air/water interface (Tardieu 1996). Many studies have shown that as VPD increases, stomatal conductance (g_s) decreases (Pezeshki and Hinckley 1982, El-

sharkawy and Cock 1984, Dang *et al.* 1997). Like ψ_{leaf}, VPD appears to be an important source of variation in g_s, however the mechanism remains unclear (Bunce 1996). Stomates close to limit E and prevent cellular drought. But are they closing in response to environmental variables, such as ψ_{soil} or VPD, or are they reacting to plant water status, that is the ψ_{leaf} itself?

Mechanisms of stomatal control

Originally, it was believed that stomates close in response to low ψ_{leaf}. This is known as the feedback response (Raschke and Kuhl 1969). In this theory, plant water status reflects environmental conditions, and regulates g_s (Boyer 1976). Proponents believe that ψ_{leaf} is crucial in determining g_s because water entry into cells (and the functioning of guard cells) is determined by ψ_{leaf}. In an experiment pressurizing the roots of Douglas fir (*Pseudotsuga menziessii*) and red alder (*Alnus rubra*), Fuchs and Livingston (1996) were able to reverse stomatal closure in dry soil (by root pressurization). They believe that the changes in ψ_{leaf} which are necessary to promote stomatal closure might be small enough as to be imperceptible by traditional measuring techniques. Using similar reasoning, Sperry *et al.* (1993) argued that leaf water potential could regulate stomatal behaviour without changing noticeably, in a manner akin to thermostat regulation.

The feedback theory of stomatal regulation has been challenged by several studies which do not show a decrease in ψ_{leaf} with increased water stress (Zhang and Davies 1989, Meinzer and Grantz 1990, Meinzer *et al.* 1992, Monteith 1995, Bunce 1996,

Tardieu 1996, Franks *et al.* 1997). Even studies which ignore the importance of enhanced g_s with increased assimilation note a static ψ_{leaf} (Nowak and Caldwell 1984, Layne and Flore 1993, Morrison and Reekie 1995). Mott and Parkhurst (1991) suggested that stomates might be able to measure relative humidity or VPD by responding to the rate of E. This would optimize photosynthesis by decreasing g_s at high rates of E, thus preserving leaf water status above the threshold for cavitation (Jones and Sutherland 1991). Indeed many studies have shown that while ψ_{leaf} does not change in relation to VPD, g_s plateaus and then decreases above a certain VPD (Meinzer and Grantz 1990, Monteith 1995, Hogg and Hurdle 1997).

Unfortunately, there is no known mechanism for guard cells to detect E or VPD. How then, do stomates sense plant water status with no measurable change in ψ_{leaf}? Stomates might sense root water status through metabolic signals, such as abscissic acid (ABA), produced in the drying roots and transported to the guard cells before a drop in ψ_{leaf} (Meinzer and Grantz 1990, Zhang and Davies 1990, Tardieu 1996). While such 'feed-forward' root signals might influence stomates during soil water deficit, they would be useless in detecting atmospheric drought. Obviously, another signal would be needed to either signal stomates directly, or incite mesophyll production of ABA. In general, there is a lack of conclusive evidence for the feed forward theory; some experiments have shown a decrease in E with increasing VPD but none have been able to demonstrate a recovery in E once VPD is decreased (Franks *et al.* 1997).

Improved water status following defoliation

When a plant is subjected to water stress, as a consequence of increased VPD or lower ψ_{soil}, it must prevent xylem cavitation while maximizing assimilation. This can be achieved by reducing stomatal conductance in the short term, or by decreasing leaf area or increasing hydraulic conductance (through increased root or xylem production) in the long term (Sperry and Pockman 1993). The last two strategies alleviate hydraulic limitations by reducing leaf level hydraulic resistance; more water is available to each leaf. Experimentally altering hydraulic conductance, either by defoliation or decreasing xylem area (cutting into sapwood or inducing embolism through air injection) should elucidate how plants recover from defoliation, and also how plants regulate water status.

An experiment by Meinzer and Grantz (1990) experimentally increased leaf specific hydraulic conductance (K_{leaf}) by defoliating sugar cane. They found that a 40% removal of leaf area caused increases in g_s so that total E and ψ_{leaf} of remaining leaf area remained the same. In a reverse approach, K_{leaf} was decreased in *Betula occidentalis* through air injection (Sperry and Pockman 1993), and xylem cutting (Sperry *et al.* 1993). Both methods resulted in an immediate decrease of g_s and E_{leaf} with no initial change in ψ_{leaf}.

Both of these studies show g_s, E_{leaf} and thus assimilation, are limited by hydraulic conductance, which in turn is affected by leaf area. If by increasing the root-to-shoot ratio, defoliation serves to increase K_{leaf}, then defoliation should augment assimilation in residual leaves, especially during water stress, when low ψ and high E mean stomates cannot normally function at maximum capacity. At high VPD, we expect fully foliated

plants to experience water stress when E exceeds the capacity of the roots and stem to provide the leaves with sufficient water (K). Defoliation should increase K_{leaf}, and thereby alleviate water stress. However, in a well watered situation with low VPD, K would not limit E, and compensatory water relations due to defoliation and increased K_{leaf} might not be evident.

Ideally, a defoliation experiment could elucidate stomatal regulation of leaf water status. If at a constant, high VPD there is an increase of g_s and E_{leaf} in residual leaves following defoliation, then pre-defoliation g_s would not have been limited by high E_{leaf}. Further, if plants were kept in well watered, constant soil environments there could be no ABA signaling effect from roots. Therefore, if stomates were inhibited prior to defoliation, they would not be responding to root signals, nor E.

My objectives were to explain the response of aspen water relations to defoliation on two levels (leaf and tree level) and under atmospheric drought. I examined leaf level water relations by measuring g_s and ψ_{leaf} in response to three levels of defoliation (none, moderate, severe) in field conditions. Tree level water relations were assessed in some of these trees by measuring sap flow through the stem. Finally, I subjected greenhouse seedlings to the same defoliation treatments under two VPD (high and low).

I predicted an increase in K_{leaf}, but not tree level K (as measured in sapflow velocity measurements) for trees subjected to defoliation. I believed the most severe defoliation would result in the highest increase in K_{leaf} since there would be a dramatic increase in the root:shoot ratio. Because of this elevated K_{leaf}, I predicted plants subjected to the most severe defoliation would demonstrate more of an increase in g_s in residual

leaves, irrespective of ψ_{leaf}. This increase in g_s, however, might not be apparent if water is not limiting. Therefore, I predicted defoliated trees, subjected to high VPD will demonstrate a larger increase in g_s than those under low VPD.

While it is clear that some plants can compensate in part for defoliation by improved water relations, it is unknown if this occurs in aspen, and if so, it is unclear how stomates sense the increased K_{leaf}. Understanding how aspen regulates its water status is essential in understanding recovery mechanisms of defoliated aspen and plant water relations in general.

Methods and Materials

Field experiments

I conducted four field experiments on small aspen trees at three locations around Edmonton, AB Canada from May to August 1997. In each experiment, I made the following measurements on trees treated with three levels of defoliation (0%, 50%, 98%).

Location	Dates	g_s	ψ_{leaf}	Sap flow	Replication
Woodbend1	04/06-16/06	X*		X	N=4
Botanical Gardens	16/06-08/07	X*	X*	X	N=4
Woodbend2	05/08-23/08	X	X	X	N=6 g_s, ψ_{leaf} N=4 sap flow
Ellerslie	19/08-07/09	X	X		N=6

*data were rejected due to instrument failure

Site description

Woodbend

The University of Alberta's Woodbend Field Station, is located 5km N of Devon, AB (53.5°N 113.4° W). It is a mixed wood site on sandy soils dominated by *Populus tremuloides* Michx. with *Pinus banksiana* Lamb., *Betula papyrifera* Marsh., and *Picea glauca* (Moench)Voss. The understory is dominated by *Amelanchier alnifolia* Nutt., *Populus tremuloides* Michx. and *Rosa spp.*

Botanical Gardens

The University of Alberta's Devonian Botanical Gardens are located 1km N of the Woodbend field station. Clones were located within the botanical garden's forest reserve which consists of 44.5 Ha of mainly *Picea glauca* (Moench)Voss. and *Pinus banksiana* Lamb. overstory. Important understory species included *Populus balsamifera* L., *Calamagrostis canadensis* (Michx.) Beauv. and *Melilotus spp.*.

Ellerslie

The third site used in my study was at The University of Alberta's experimental farm at Ellerslie located 20km S of Edmonton (53.5°N 113.4° W). It is mostly cultivated, chernozemic soil with isolated groves of *Populus tremuloides* Michx. and *Populus balsamifera* L.. Understory includes *Rosa spp.*, *Symphoricarpos albus* (L.)Blake, and *Populus tremuloides* Michx.. All clones were selected from a uniform, west-facing aspect.

Clone selection and defoliation treatments

Clones at each site were selected as replicates on the basis of phenology, stem and bark characteristics. Both clones and trees within clones were selected to minimize variation in tree age, size and exposure. Within each clone, I selected three similar, proximal individuals to receive the three treatments of 98% defoliation, 50% defoliation, and 0% defoliation. At each site, I measured stomatal conductance during four days: day of defoliation, prior to leaf removal (pre-defoliation), first day after defoliation (post-defoliation 1), third day after defoliation (post-defoliation 3 Ellerslie) or fifth day after

defoliation (post-defoliation 5 Woodbend2), and nineteenth day after defoliation (post defoliation 19).

Control trees were left intact, with no leaf removal. The 50% defoliated trees had the leaves of every second short shoot removed by hand by tearing at the apex of leaf petioles. The 98% treatment required that all leaves except those from 10 to 15 short shoots be removed; the actual number varied depending on the size of the canopy. All removed leaves were bagged and leaf area was determined using a Li-Cor Model 3100 Area Meter. Finally, at each site, I recorded hourly averages of temperature and relative humidity within the clones at approximately 1.5m using a CR21X datalogger (Campell Scientific Equipment Ltd.).

Total leaf area was measured for all trees in all treatments at Woodbend1 and Botanical Gardens, but was estimated for Ellerslie and Woodbend2. Data from Woodbend1 and the Botanical Gardens indicated that 98% (SE=0.50) and 49% (SE=2.49) of the total leaf area was removed during defoliation for the respective treatments. Using these figures, I estimated total leaf area for the 50% defoliated trees in Ellerslie and Woodbend2 to be twice the removed leaf area . For the 98% defoliated trees, total leaf area was determined as 1.02 times the removed leaf area. Finally, total leaf area of each control tree was calculated to be the average of the calculated total leaf area of the 50% and 98% trees in that clone. Residual leaf area for Ellerslie and Woodbend2 was estimated to be the difference between the calculated leaf area and the measured leaf area removed.

Stomatal conductance

Stomatal conductance was measured for each tree using a Li-Cor 1600 Steady State Porometer. Stomatal conductance measurements were performed at Woodbend2 (August 5, 6, 10 and 23) and Ellerslie (August 19, 20, 22 and September 7). At all sites, only open grown, young aspen less than 6m tall and with a diameter of at least 5 cm were selected for measurement. All measurements were performed at midday (12:00 - 15:00) on warm, sunny days, in full light. I arbitrarily selected 4 leaves from 4 different short shoots on each tree for measurement. Each tree was measured in less than five minutes. As I measured stomatal conductance for each tree, an assistant simultaneously measured leaf water potential using a P.M.S. Scholander pressure bomb. To conserve leaf area on 98% trees, only two short shoots were measured per tree for each water potential reading.

Sap flow

I conducted measurements of sap flow based on a method by Swanson (1983) modified by Hogg and Hurdle (1997) on three occasions at three of the previously described sites: Woodbend1 (June 4 -16), at the Botanical Gardens (June 16 - July 8), and again at Woodbend2 (July 8 - August 24).

At each site I randomly selected four clones from the six previously selected clones that were used for stomatal conductance measurements. At each clone, I assembled heat pulse instrumentation for the three trees (control, 50%, 98%). Sap flow was monitored once an hour for the period of study by the following method: all installations were located on the north side of the tree, 20-30 cm above the ground. Two thermocouples were inserted approximately 1cm into the sap wood, 0.75 cm above (TC_{up}) and below

(TC_{low}) a 5cm brass heater (2W/cm). Another thermocouple, the reference (TC_{ref}), was positioned outside the plane of the heater and the other thermocouples. A high precision of distances and diameters was ensured by using a steel template to guide the drill at each tree. The sap flow installations were then swathed in thin polystyrene foam to protect the instruments from direct insolation. The heater was powered for the first 4 seconds of every hour. Damaged heaters and thermocouples were replaced as needed. A CR10 data logger recorded the temperature difference between the TC_{up} and TC_{ref}, and the difference between the TC_{low} and TC_{ref} at 1, 2, and 3 minutes following the hourly heat pulse. The system was powered by a battery which was continuously recharged by a solar panel.

An uncorrected sap flow was calculated by using the following equation from Hogg and Hurdle (1997):

$$S = 4.36\ln(TC_{up}/TC_{low}),$$

where S = sap flow in cm/hr, and 4.36 is a generalized constant based on thermal wood conductivity ($0.38 Jm^{-1}s^{-1} \cdot C^{-1}$), bulk density ($0.37 g/cm^3$) and gravimetric water content of 100% functional sap wood in aspen.

For all trees, sap flow was corrected to have a minimum night time value of zero. In these trees, the most negative value was added to all other values. Further corrections were applied to trees demonstrating large "spikes" in S. These data points were largely isolated and were omitted from further analysis. In the case of Woodbend2 "M", S values at 11:00 were consistently spiked, and were deleted from the analyses. A regular spike

interval indicates possible heating of the sapwood by midday sun (E. Hogg, personal communication).

Growth Chamber Experiment

Seedling Preparation

I obtained 97, plug+1 *Populus tremuloides* Michx. seedlings in early December 1997. These were placed in the dark in cold storage for one week, then planted in six inch pots in a 1:2 mixture of sand and MetroMix, and placed in a growth chamber at 20°C, 40% R.H., 300μmol light and 18 hour days for 35 days until full expansion of preformed leaves (7 weeks). Trees were well watered and fertilized using a 20-20-20 N-P-K formulation. Prior to defoliation treatment, stomatal conductance was tested on the trees to ensure recovery from planting shock. Subsequently, the 48 trees with highest stomatal conductance were selected for the experiment and randomly assigned to treatments.

Water relations under two levels of humidity

Trees were subjected to three levels of defoliation (control, 50% and 95%) and two levels of humidity (80% RH or VPD=0.64 kPa, and 40% RH or VPD= 1.9kPa at 25°C both at 1000μmol m^{-2} s^{-1} of light). Humidity treatments were applied by two growth chambers (EGC Type M12 by Environmental Growth Chamber of Chagrin Fall, Ohio). Inner chamber dimensions were approximately 2.5m x 1.28m x 1.95m high. In this experiment, 50% defoliation consisted of removing every second leaf, and all but 7 leaves were removed for the 95% treatment. Each plant was randomly assigned to one of the six treatments, and moved to humidity treatment chambers the night before ecophysiological

measurements. Trees were immediately returned to common, pre- humidity treatment conditions following measurement.

I measured stomatal conductance and leaf water potential on the same plants on three days (pre-defoliation, 2 and 8 days post-defoliation). Assimilation and stomatal conductance were measured using a CIRAS infra-red gas analyzer. Two leaves were tagged and measured for all days. However, due to the effect of measurement time spent outside the humidity chamber, only the first measurement of each day was considered for further analysis. Leaf water potential was measured concurrently on one leaf per tree using a P.M.S Scholander pressure bomb.

Data analysis

For all experiments, the variable examined statistically was the difference between pre-defoliation measurements and each subsequent measurement. The student-Neumann-Keuls method of means separation was used for all analyses.

Sap flow

To analyze the changes in sap flow, I calculated a daily average pre-defoliation (S_{PRE}) and post-defoliation S (S_{POST}) for all trees. By subtracting S_{PRE} from S_{POST}, I obtained three values for each clone: difference98%, difference50% and difference control, which were then analyzed using a Completely Randomized Design, two-way ANOVA (SAS Institute Inc. 1987). In this model, my two between subjects factors were clone and defoliation level.

Ellerslie

For stomatal conductance and leaf water potential measurements at Ellerslie, I rejected post-defoliation 19 (September 7) since senescence had begun in many of the trees. By subtracting pre-defoliation measurements from each 1 and 3 days post-defoliation, I obtained two values for each tree: difference1 and difference3. Having only two data points, I used a split-plot, two-way ANOVA (SAS Institute Inc. 1987), with clone and treatment being my between subjects factors, and time a within subjects factor.

Woodbend2

I did not analyze the stomatal conductance and leaf water potential data for Woodbend2. During my measurements, daily temperatures exceeded the maximum cuvette temperature and minimum cuvette humidity for the proper functioning of the Li-Cor 1600 porometer.

Greenhouse

I subtracted my pre-defoliation assimilation, stomatal conductance and leaf water potential measurements from my post-defoliation measurements on days 2 and 8 post-defoliation, and obtained difference2 and difference8. These data were treated as a split-plot, with two between subject factors (humidity and treatment), and one within subjects factor (time). To test the effect of cuvette humidity on stomatal conductance of high humidity plants, I measured two leaves from six plants with low cuvette humidity (8 millibars) and again with high cuvette humidity (10 millibars). I performed a paired t-test on the results using SAS system (*SAS Institute* Inc. 1987).

Results

1. Field Experiments

I examined the responses of stomatal conductance and leaf water potential (ψ_{leaf}) to three levels of defoliation in the field at Ellerslie, AB.

1.A. *Stomatal conductance*

1.A.i. *Pre- and post-defoliation*

Increased stomatal conductance was apparent in 50% and 98% defoliated aspen in the field, at Ellerslie ($p=0.0008$)(figure 1). Though all defoliation treatments exhibited similar pre-defoliation values, those subjected to 50% defoliation increased to 400 mmol m^{-2} s^{-1} on day 1 post-defoliation and remained elevated on day 3. Similarly, plants with 98% defoliation increased to 418 mmol m^{-2} s^{-1} on day 1 and remained elevated on day 3. In contrast, stomatal conductance decreased to 314 mmol m^{-2} s^{-1} in undefoliated aspen. Stomatal conductance in 50% and 98% defoliated plants was not significantly different (SNK, $p<0.05$). Mean values for all defoliation treatments are tabulated in Appendix 6.

1.A.ii. *Magnitude of change*

The change in stomatal conductance following defoliation (i.e. post-treatment minus pre-treatment values) for each treatment is shown in figure 2. There was a significant increase in stomatal conductance for 50% and 98% defoliated trees following defoliation at Ellerslie ($p=0.0017$). The 98% defoliation treatment resulted in an immediate increase of 105 mmol m^{-2} s^{-1} that was maintained until day 8. The 50% treatment

increased by 84 mmol m^{-2} s^{-1} on day 1, and by day 3 had increased a total of 88 mmol m^{-2} s^{-1} from pre-defoliation values. Control trees initially increased slightly (17 mmol m^{-2} s^{-1}), but decreased overall by day 3 (-3 mmol m^{-2} s^{-1}). There was no significant difference between the amount of increase in 50% and 98% treatments (SNK,$p<0.05$), or between days 1 and 3 ($p=0.42$).

1.B. *Leaf water potential*

1.B.i. *Pre- and post-defoliation*

Leaf water potential (ψ_L) did not change in response to defoliation ($p=0.19$) (figure 3). On day 3, ψ_{leaf} was -1.62 for both 50% and 98% defoliation treatments. Leaf water potential in trees with 50% and 98% defoliation was not significantly different post-defoliation (SNK, $p<0.05$). For trees with 0% defoliation, ψ_{leaf} remained static on day 1, but dropped to -1.86 MPa on day 3. Mean ψ_{leaf} for all measurements at Ellerslie are tabulated in Appendix 7.

1.B.ii. *Magnitude of change*

The differences of ψ_{leaf} from pre-defoliation were relatively unchanged on day 1 for all treatments but by day 3, 50% defoliated trees became less negative by 0.05 MPa, while 98% defoliated trees became more negative by 0.07 MPa, and control by 0.3 MPa (figure 4). However, these changes were not significant ($p=0.19$), and defoliation treatments were not significantly distinguishable (SNK, $p<0.05$). In addition, there was no difference between changes of ψ_{leaf} on days 1 and 3 ($p=0.24$).

1.C. *Sap flow*

I measured tree-level sap flow (S_T) in the field for trees subjected to three levels of defoliation (0%, 50% and 98%). Measurements were conducted at Woodbend 2 and Botanical Gardens.

Sap flow decreased after defoliation for trees subjected to 98% defoliation ($p= 0.074$). Figure 5 shows the typical sap flow signature over time for three defoliation treatments at botanical gardens (5a) and Woodbend 2 (5b). Sap flow velocity for 0% defoliation trees (figures 5ai and 5bi) was unpreturbed by defoliation on day 185, with some trees even increasing slightly after the day of defoliation (Appendix 1). Trees subjected to 50% defoliation showed lower daily maximums after defoliation (figures 5ai and 5bii), but the average daily sap flow decreased only slightly (Appendix 1). Trees subjected to 98% defoliation showed a greatly reduced daily flux, with no recognizable diurnal pattern (figures 5aiii and 5biii). The trees in this treatment show severely reduced post-defoliation sap flow (Appendix 1).

Trees at all sites showed a large decrease in tree-level sap flow (δS_T) following 98% defoliation (3.46 cm/h at Woodbend 2, and 1.84 cm/h at Botanical Gardens)(figures 6a and 6b), and a smaller δS_T for trees with 50% defoliation was evident in both sites (1.90 cm/h Woodbend 2, and 1.12 cm/h Botanical Gardens). Trees with 0% defoliation decreased very slightly post-defoliation (0.76 cm/h at Woodbend, and 0.56 cm/h at Botanical Gardens).

2. Controlled environment chambers

I measured the response of aspen seedlings under two vapour pressure deficits (VPD) (1.9 kPa and 0.64 kPa) and three defoliation levels (0%, 50% and 98%). Stomatal conductance, $C0_2$ assimilation and leaf water potential were measured prior to defoliation, and two and eight days following defoliation.

2.A. *Stomatal conductance*

2.A.i. *Pre- and post-defoliation*

Green house results indicated a pattern of compensatory stomatal conductance similar to that shown in Ellerslie, with 50% and 98% defoliated seedlings demonstrating compensatory stomatal conductance post-defoliation (figure 7). The values for all defoliation treatments were lower under high VPD ($p=0.0024$). Under high VPD, the highest mean values of stomatal conductance were 64 mmol m^{-2} s^{-1} for 0% defoliation, 85 mmol m^{-2} s^{-1} for 50% defoliation, and 97 mmol m^{-2} s^{-1} for 98% defoliation. Under the low VPD treatment, maximum values of stomatal conductance were much higher: 255 mmol m^{-2} s^{-1} (0% defoliation), 303 mmol m^{-2} s^{-1} (50% defoliated), and 325 mmol m^{-2} s^{-1} (98% defoliated). Mean stomatal conductance values for all defoliation and VPD treatments are tabulated in Appendix 8.

2.A.ii. *Magnitude of change*

When looking at the difference from pre-defoliation, the trend for compensatory stomatal conductance becomes apparent for both VPD treatments (figure 8). For high VPD, 50% defoliation resulted in an increase of 50 mmol m^{-2} s^{-1} and 98% resulted in an increase of 42 mmol m^{-2} s^{-1}. At low VPD, the 50% seedlings increased by a maximum of

165 mmol m^{-2} s^{-1} and 98% defoliated seedlings by 164 mmol m^{-2} s^{-1}. Here, the defoliation effect was highly significant ($p=0.0042$), with no significant difference between the amount of increase for 50% and 98% defoliation treatments (SNK, $p<0.05$). Like the pre- and post-defoliation values, the amount of increase in stomatal conductance after defoliation was affected by VPD treatments, with the amount of increase for 50% and 98% defoliation much lower under high VPD. As in the field experiment, there was no significant difference between the amount of increase on either day ($p=0.93$).

2.A.iii. *Relative change*

Stomatal conductance of seedlings in both VPD treatments showed similar increases in response to defoliation when expressed as a per cent of their initial stomatal conductance (figure 9). The overall, relative change from pre-defoliation (% of day 0) after defoliation treatments for stomatal conductance was not apparently different between the VPD treatments, despite having a much greater magnitude of change at low VPD (figure 8). In fact, relative increases in stomatal conductance under high VPD exceeded those under low VPD for all defoliation treatments on day 2, and for all but the 98% defoliated seedlings on day 8. The relative increase was lowest for 0% defoliated seedlings in both treatments (minimum values were 59% for high VPD and 34% for low VPD on day 2), and highest for 50% defoliated seedlings (174% for high VPD and 139% for low VPD on day 8). While there was a trend for larger increases at 50% defoliation, the defoliation treatments were not significantly different from one another ($p=0.69$). The

overall, relative difference was significantly higher on day 8 for both VPD, and all defoliation treatments ($p=0.0061$).

2.B. *$C0_2$ Assimilation*

2.B.i. *Pre- and post-defoliation*

Assimilation, like stomatal conductance, was much lower under high VPD (figure 10). The largest mean values for the high VPD treatment were 5.75 μmol m^{-2} s^{-1} (0% defoliation on day 2), 6.05 μmol m^{-2} s^{-1} (50% defoliation on day 2), and 7.47 μmol m^{-2} s^{-1} (98% defoliated on day 8). Under low VPD, the largest mean values were higher: 8.9 μmol m^{-2} s^{-1}(0% defoliated), 12.0 μmol m^{-2} s^{-1} (50% defoliated), and 12.3 μmol m^{-2} s^{-1} (98% defoliated). Seedlings subjected to 98% defoliation increased more than seedlings with 50% defoliation, and 0% defoliated seedlings showed no compensatory response at all. The differences between defoliation treatments were significant ($p=0.040$), and each differed significantly from the others (SNK, $p<0.05$). Mean values for $C0_2$ assimilation values for all defoliation and VPD treatments are tabulated in Appendix 10.

2.B.ii. *Magnitude of change*

Though pre- and post-defoliation values of assimilation differed under the VPD treatments, changes from pre-defoliation were apparently unaffected by VPD (figure 11). In both VPD treatments, seedlings with 50% and 98% defoliation showed greater increases in assimilation following defoliation ($p=0.023$).

Under high VPD, assimilation increased and remained elevated for both 50% and 98% defoliated seedlings. Those subjected to 50% defoliation increased by 1.6 μmol m^{-2} s^{-1} compared to 3.0 μmol m^{-2} s^{-1} for 98% defoliated seedlings over pre-defoliation values.

For the low VPD treatment, however, 50% defoliated seedlings increased initially, but decreased to the pre-defoliation value of 9.3 μmol m^{-2} $^{-1}$ by day 8. Seedlings with 98% defoliation increased by 2.9 μmol m^{-2} s^{-1} on day 2, then decreased by 0.7 μmol m^{-2} s^{-1} on day 8. There was no significant difference between the amount of increase in 50% and 98% treatments following defoliation for either VPD treatment (SNK, $p<0.05$). In contrast, there was no increase in assimilation of 0% defoliated seedlings. In fact, after an initial increase on day 2 for both VPD treatments, seedlings with 0% defoliation on day 8 had rates of assimilation that were lower than pre-defoliation values. For both VPD and all defoliation treatments, increases in assimilation were significantly greater on day 2 ($p=0.015$).

2.B.iii. *Relative change*

There was a marked difference between relative changes at low and high VPD (figure 12). In this case, relative increases in assimilation were much higher under high VPD. Maximum relative increase under high VPD was 97.9% (98% defoliation on day 8), but only 38.2% under low VPD (98% defoliation day 2). Considering initial differences between the VPD treatments for assimilation, and since seedlings in both VPD treatments show a similar gross change, those subjected to high VPD had a much larger relative change after defoliation. There was no significant difference between defoliation treatments ($p=0.30$). Increases for both VPD treatments and all defoliation treatments (excluding high VPD, 98% defoliation) were higher on day 2 ($p=0.034$).

2.C. *Leaf water potential* (ψ_{leaf})

2.C.i. *Pre- and post-defoliation*

Leaf water potential was less negative under high VPD (p=0.0034) (figure 13). The differences between high and low VPD treatments, however, were small: the most negative mean values under high VPD were -1.38 MPa (0% defoliation), -1.24 MPa (50% defoliation), and -1.15 MPa (98% defoliation). Under low VPD, the most negative mean values were -1.60 MPa (0% defoliation on day 2), -1.58 MPa (50% defoliation on day 2), and -1.44 MPa (98% defoliation on day 0). Defoliation treatments differed significantly for pre- and post-defoliation under both VPD treatments; 0% and 50% defoliated seedlings were most negative, while 98% defoliated seedlings were slightly less so (p=0.019, SNK $p<0.05$). Mean ψ_{leaf} values for all defoliation and VPD treatments are tabulated in Appendix 9.

2.C.ii. *Magnitude of Change*

Here, greenhouse results support findings in the field, as there was no significant defoliation effect on greenhouse ψ_{leaf} (p=0.19) (figure 14). Under high VPD, all treatments showed a tendency to became more negative; 0% and 50% defoliated seedlings showed a recovery to pre-defoliation levels at day 8, while 98% defoliated seedlings became less negative on day 8. Under low VPD, the pattern was similar, but 0% and 50% defoliated seedlings did not recover on day 8, and 98% defoliated seedlings became less negative on days 2 and 8. However, there was no significant difference in the changes of ψ_{leaf} between days 2 and 8 (p=0.35).

2.C.iii. *Relative change*

The overall, relative change in leaf water potential was not affected by defoliation treatment (p=0.55), nor VPD treatment (figure 15). However, as in magnitude of change,

98% defoliated seedlings appeared to be less negative, and were statistically segregated from 0% and 50% defoliated seedlings (SNK, $p<0.05$). Leaf water potential in both VPD and all defoliation treatments became more negative on day 2 ($p=0.034$).

Discussion

Field Experiments

1. Stomatal conductance and leaf water potential

Compensatory stomatal conductance was clearly evident for both 50% and 98% defoliated trees. This response to defoliation has been documented in other species (Bassman and Dickmann 1982 (*Populus x euramericana*), Heichel and Turner 1983 (*Quercus rubra* and *Acer rubrum*), Layne and Flore 1993 (*Prunus cerasus*), Morrison and Reekie 1995 (*Oenothera biennis*), Paez and Gonzalez 1995 (guinea grass)). This means that a defoliation event would not be as devastating to a tree as would be expected by assessing leaf loss alone. It is important to note that despite a large difference in leaf area, trees subjected to 50% and 98% defoliation did not differ with respect to amount of compensatory stomatal conductance. Therefore despite similar leaf-level compensation, the amount of compensation on a tree-level would be much smaller for 98% defoliated trees. However, despite the greatly reduced leaf area in the 98% defoliated trees, the increased stomatal conductance might be sufficient to compensate for respiration costs, and maintain the tree until a new leaves are produced (this occurred approximately 10 weeks following defoliation for both defoliation levels).

The observed compensatory stomatal conductance, along with other factors such as increased leaf-level PAR, might be enough to maintain net tree assimilation rates for trees with moderate (50%) defoliation. Because of the relatively large residual leaf area (50% defoliated trees were difficult to visually differentiate from 0% defoliated trees in the field), moderate defoliation could have little impact on annual growth. In a study by

Bassman *et al.* (1982) on nursery-grown, hybrid poplars subjected to varying defoliation intensity found that moderate defoliation (up to 40%) had a negligible effect on growth (height and basal diameter). In the present study, the remaining leaf area on 50% defoliated trees might have been sufficient given the advantage of increased root:shoot ratio along with other benefits of defoliation, such as decreased shading on residual leaves and less resource competition among leaves.

The similarity of the increase in stomatal conductance following defoliation in 50% and 98% defoliated trees might indicate a limit to the compensatory response. Meinzner and Grantz (1990) also found that sugar cane showed increasing stomatal conductance (leaf-level) in response to removal of 20-40% of total leaf area, but the effects of more severe defoliation were not examined. In the present study, it is possible that there was not enough soil water to fully supply the newly increased leaf-level, hydraulic conductance and realize the potential for maximal compensatory stomatal conductance following 98% defoliation. Alternatively, the limit to compensatory stomatal conductance could be due to physical constraints: stomates might be at maximum aperture at 50% defoliation, or water potential differences at the branch insertions might limit the amount of water flowing to the leaves, regardless of soil water status.

It is unlikely that leaf water potential limited the compensatory response because there was no statistically significant response of defoliation on ψ_{leaf}. This response has been observed in other studies, and it is generally accepted that ψ_{leaf} does not directly control stomatal behaviour (Farquhar 1978, Grantz 1990, Mott and Parkhurst 1991, Bunce 1996). In the defoliation experiment on sugar cane, Meinzer and Grantz (1990)

found that stomatal conductance increased with increasing defoliation to maintain the pre-defoliation ratio of water loss:water transport capacity. This resulted in a ψ_{leaf} which was constant over a variety of leaf areas.

2. Sap flow

Sap flow did not noticeably decrease in 50% defoliated trees. Despite having only half the leaf area of 0% defoliated trees, trees with 50% defoliation maintained sap flow that was not significantly different from those with 0% defoliation. Trees with 98% defoliation, however, showed a marked decrease in total sap flow, suggesting there were simply not enough leaves to use the available water. This further supports the theory that trees experiencing moderate defoliation would not experience loss of annual growth due to a single defoliation event, since trees with 50% defoliation were still able to use a similar amount of water (and thus presumably fix a similar amount of carbon) as trees with no defoliation.

Controlled environmental conditions

1. Stomatal conductance and ψ_{leaf}

The response of stomatal conductance to defoliation under controlled environmental conditions was very similar to the response observed in the field, at Ellerslie. In both cases, compensatory stomatal conductance was evident for seedlings with 50% and 98% defoliation (figure 7). Like the field experiment, seedlings with 50% and 98% defoliation showed similar increases in stomatal conductance. Unlike the field

experiment, seedlings with 0% defoliation showed an increase in stomatal conductance following defoliation, and the compensatory response of all defoliation treatments increased more on day 8. The reasons for these increases are unclear; most likely they indicate the seedlings had not yet reached full root development after transplanting.

The compensatory response of seedlings with 98% defoliation was accompanied by a ψ_{leaf} that was significantly less negative than the other defoliation treatments (figure 13). This contrasts with the field experiment, and other studies which have shown that ψ_{leaf} does not change with stomatal conductance (Meinzer *et al.* 1992, Sperry and Pockman 1993, Dang *et al.* 1997). The ψ_{leaf} for 98% defoliated seedlings may have only appeared high in comparison to the more negative ψ_{leaf} of seedlings with 0% and 50% defoliation which may have depleted soil moisture stores more rapidly. However, in this situation, soil water was not limiting. All seedlings were watered to saturation the night previous to measurement. Since there was no overall defoliation effect on ψ_{leaf} (figure 14), it is unlikely that the less negative ψ_{leaf} for trees with 98% defoliation was due to the defoliation treatment.

Like the field experiment, there was an apparent limit to the compensatory response. In this case, it is unlikely 98% defoliated seedlings failed to maximize potential gains in leaf-level hydraulic conductance because of insufficient soil moisture since soil water was constant and well watered throughout the experiment. More likely, physical limitations of the stomates or hydraulic architecture constrained stomatal conductance in these seedlings.

2. Response of stomatal conductance and ψ_{leaf} to VPD

Seedlings grown under high VPD had lower rates of stomatal conductance than those exposed to low VPD. Stomatal conductance has been shown in many species to decrease with increasing VPD (Pezeshki and Hinckley 1982, El-sharkway and Cock 1984, Syvestren 1984, Grantz 1990, Monteith 1995, Dang *et al.* 1997, Hogg and Hurdle 1997). Contrary to my hypothesis, the change in stomatal conductance in response to defoliation was much greater for seedlings exposed to low VPD. Therefore, the apparent limit to the compensatory stomatal conductance at 50% defoliation at Ellerslie and in the green house was not due to insufficient supply of, or demand for, moisture. However, despite lower overall values and a smaller compensatory response after defoliation, seedlings grown under high VPD changed in the same proportion to those grown under low VPD. This suggests that the compensatory response was contingent on initial rate of transpiration or stomatal conductance, and not on severity of defoliation. Sperry *et al.* (1993), in a 'reverse defoliation' experiment, reduced hydraulic conductance in birch by severing stem xylem tissue. They found the factor most responsible for determining adjustment to the reduced water flow was the rate of transpiration at the time of defoliation. Trees with very high transpiration were not able to adjust, while those with a moderate rate of transpiration survived.

In contrast to the field experiment, ψ_{leaf} for seedlings subjected to low VPD was significantly more negative. Considering these seedlings had the highest rates of stomatal conductance, it was assumed they should have the least negative ψ_{leaf}. This discrepancy of less negative ψ_{leaf} in seedlings subjected to high VPD might be the end result of a feedback

loop (Tardieu *et al.* 1996). Low stomatal conductance under high VPD would result in reduced net assimilation, which would lead to even lower rates of stomatal conductance. As a result, ψ_{leaf} would become less negative.

3. $C0_2$ Assimilation

Seedlings subjected to 50% and 98% defoliation exhibited compensatory leaf-level, net photosynthesis. Unlike the stomatal conductance response, however, seedlings with 98% defoliation showed significantly greater compensation. Since assimilation and stomatal conductance are linked, yet not predicted exclusively by one another, it is reasonable that they should respond differently to defoliation. For example, seedlings with 98% defoliation had less leaf shading and relatively more nutrients available to each leaf than would seedlings with 50% defoliation. Several studies have reported an increased nitrogen concentration (which is directly related to $C0_2$ assimilation activity) in residual leaves of defoliated seedlings due to fewer nutrient sinks (Nowak and Caldwell 1984, von Caemmerer and Farquhar 1984). As well, severe defoliation might create a stronger demand for assimilate (Layne and Flore 1993, Ovsaka *et al.* 1992).

It is noteworthy that unlike the stomatal conductance of 0% defoliated seedlings, there was no net increase in $C0_2$ uptake for 0% defoliated seedlings after defoliation, despite a simultaneous increase in stomatal conductance. It is possible that despite the immaturity of the root system at the start of the experiment, stomatal conductance was not limiting $C0_2$ assimilation, and other limitations to $C0_2$ uptake (leaf shading, nutrient status) were exacerbated by the lack of defoliation.

4. Response of $C0_2$ assimilation to VPD

High VPD had a smaller relative impact on the rate of $C0_2$ assimilation than on stomatal conductance. Like stomatal conductance, assimilation was lower under high VPD. This agrees with many other studies which have reported a similar depressing influence of increasing VPD on the rate of assimilation (Pezeshki and Hinckley 1982, Syvestren 1994, Dang *et al.* 1997). However, this is an indirect response to VPD; the concurrent reduction in stomatal conductance reduces the concentration of intercellular $C0_2$ and ultimately causes assimilation to decrease with increasing VPD.

The reaction of $C0_2$ assimilation to defoliation under low and high VPD was very different than stomatal conductance. $C0_2$ assimilation of seedlings exposed to high VPD changed in a greater proportion after defoliation than those under low VPD (figure 12). It is possible that the seedlings under low VPD did not increase as much because they were already assimilating at maximum capacity prior to defoliation, while seedlings exposed to high VPD were limited in $C0_2$ uptake by low stomatal conductance. Thus the seedlings grown under high VPD had more to gain from a compensatory stomatal conductance following defoliation.

Evidence for stomates responding to the rate of transpiration

Both in the field and controlled environment chambers, there is evidence that stomates responded immediately to an increase in leaf-level hydraulic conductance by increasing the rate of stomatal conductance. Implicit in this discussion is that the stomates

are somehow able to sense the increased hydraulic conductance. Unfortunately, the mechanism which signals stomates to open and close is unclear.

In the present study, it is unlikely that ψ_{leaf} had any direct signaling effect on the stomates in these experiments because ψ_{leaf} remained statistically unchanged after defoliation despite significant increases in stomatal conductance. Under controlled environmental conditions, stomatal conductance demonstrated a similar proportional increase in both VPD treatments, despite having statistically less negative ψ_{leaf} under high VPD. Further, stomatal conductance was not inhibited low ψ_{leaf} for seedlings under low VPD.

It is also unlikely that a chemical messenger, such as ABA, acted as a signal due to the constant, watered condition of the soil in the controlled environment experiment. Furthermore, this mechanism does not explain the effects of atmospheric drought. This area requires more research, specifically the effect of high VPD on the mesophyll production of ABA.

There are, however, indications that stomates might be responding to the rate of transpiration at the leaf-level. Firstly, the seedlings exposed to high VPD exhibited much lower conductance, but had a stronger evaporative demand than those exposed to low VPD. Thus it is conceivable that seedlings in both treatments were transpiring at a similar rate. Since there was no difference in the relative increase in stomatal conductance after defoliation for VPD treatments, it is possible that all seedlings were transpiring at the maximum rate possible prior to defoliation. Thus any compensatory increases would be the result of an increased transpirational capacity, which would be similar for both VPD

treatments. Finally, the apparent limit to the compensatory stomatal response might also be explained by this theory. Hogg and Hurdle (1997) found evidence for an upper limit to the transpiration rate in aspen. If there is a transpiration threshold (above which water loss exceeds water transport capacity and xylem cavitation ensues), it is fathomable that if residual leaves on seedlings subjected to 50% defoliation are transpiring at the threshold, further defoliation would not incite greater compensation.

Conclusions

I found evidence for compensatory stomatal conductance and CO_2 assimilation following defoliation in aspen. Thus, a 50% defoliation event would not result in a 50% loss of assimilation capacity. However, the recovery capacity observed in this experiment was insufficient to maintain pre-defoliation tree-level, net conductance and assimilation. Therefore, the aspen in this study would be negatively affected by a single defoliation event. Sap flow measurements indicated that trees subjected to moderate (50%) defoliation might show adequate recovery after a defoliation event, since total tree transpiration decreased only slightly following defoliation. However, in nature, defoliation by forest tent caterpillars is often severe, in which case tree-level compensation is greatly limited.

More significant in the recovery of aspen to defoliation might be the enhancement of photosynthesis in new leaves. It would be useful to compare the CO_2 assimilation rates and water relations of these leaves with rates in residual leaves. In addition, since forest tent caterpillar infestations often occur in sequential years, the full recovery response of aspen cannot be understood by examining a single season of defoliation. The response of trees subjected to multiple years of defoliation might reveal long-term recovery strategies, such as a clonal response. Since the extent and degree of interclonal connections is unknown, undefoliated trees might have a role in 'supporting' defoliated trees. It is possible that the compensatory responses at the individual tree-level in the field were in some way affected by the size and or condition of the entire clone.

This experiment could benefit from direct measurements of annual increment (by obtaining discs from trees subjected to different intensities and frequencies of defoliation) to quantify the impact of compensatory responses on the annual growth. This information could help silviculturists predict harvest schedules for stands subjected to defoliation events. For example, stands with moderate defoliation might show adequate mean annual increment after a defoliation event, whereas severely defoliated stands might require more immediate harvest. This information can also be used to understand the phenomenon of aspen dieback. It is possible that certain intensities and frequencies of defoliation do not greatly compromise annual growth, and do not predispose aspen to dieback. If this is true, then there are also implications for control of defoliating insects. If moderate defoliation is not detrimental to annual growth, then perhaps control strategies focusing on decreasing the density of defoliators would be sufficient.

This study clearly demonstrated the surpressing effect of high VPD on stomatal conductance and CO_2 assimilation in aspen. This has serious implications for aspen if the predicted climate warming becomes a reality. In the proposed drier, hotter climate of the aspen park land and boreal forest, the increased VPD could significantly decrease the productivity of aspen. If more frequent defoliation events are part of the new climate, as is also predicted (Hogg and Hurdle 1995), then aspen productivity would be further compromised, since our study demonstrated only a limited capacity for tree-level compensation following severe defoliation.

Finally, the results from this study provided insight into the mechanism controlling the compensatory stomatal response. Of the current theories, it is possible the stomates in

this study were responding to the rate of transpiration at the leaf-level. This was partly explained by the failure of ψ_{leaf} to change with stomatal conductance, and an apparent limit to the compensatory response at 50% defoliation. To clarify the importance of this limit, and to identify the supposed threshold transpiration rate for aspen, it would be valuable to obtain direct measures of transpiration at the leaf level, and determine more precisely the per cent of defoliation beyond which there are no further increases in stomatal conductance and $C0_2$ assimilation at the leaf level.

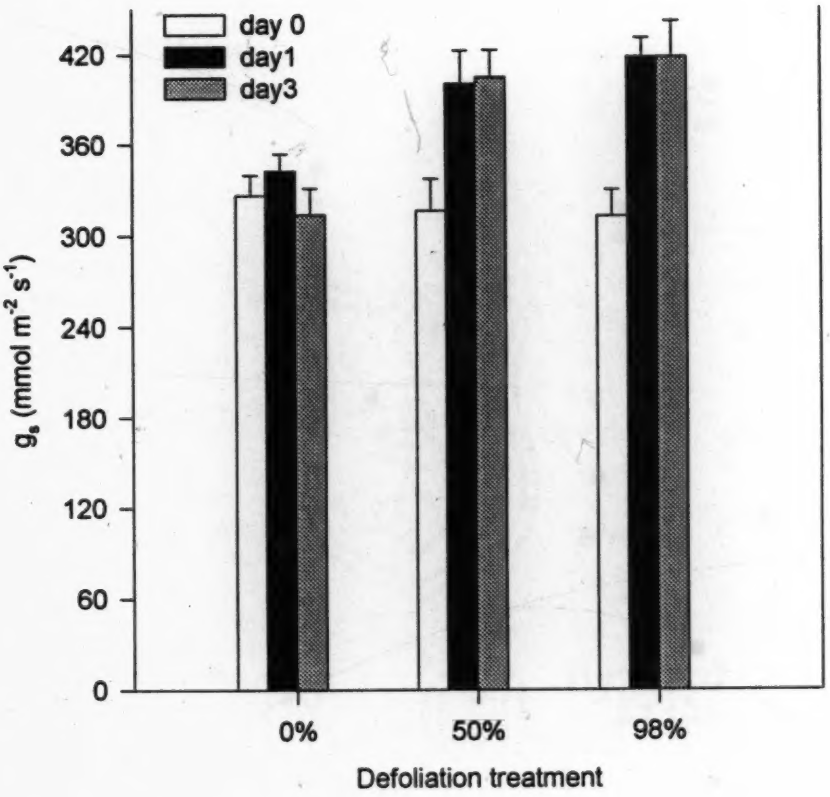

Figure 1: Pre- and post-defoliation stomatal conductance for three defoliation levels measured in the field at Ellerslie

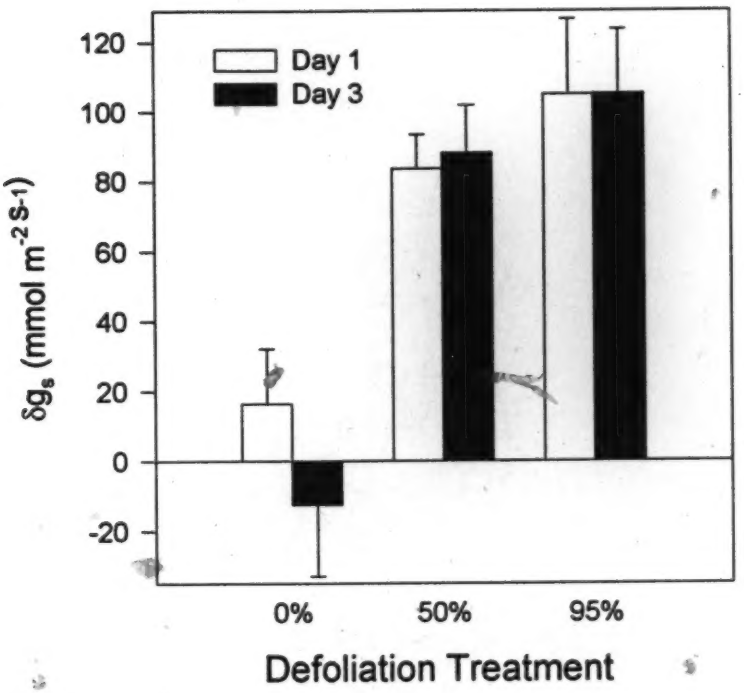

Figure 2: Change in stomatal conductance from pre-defoliation for three defoliation levels, measured in the field at Ellerslie.

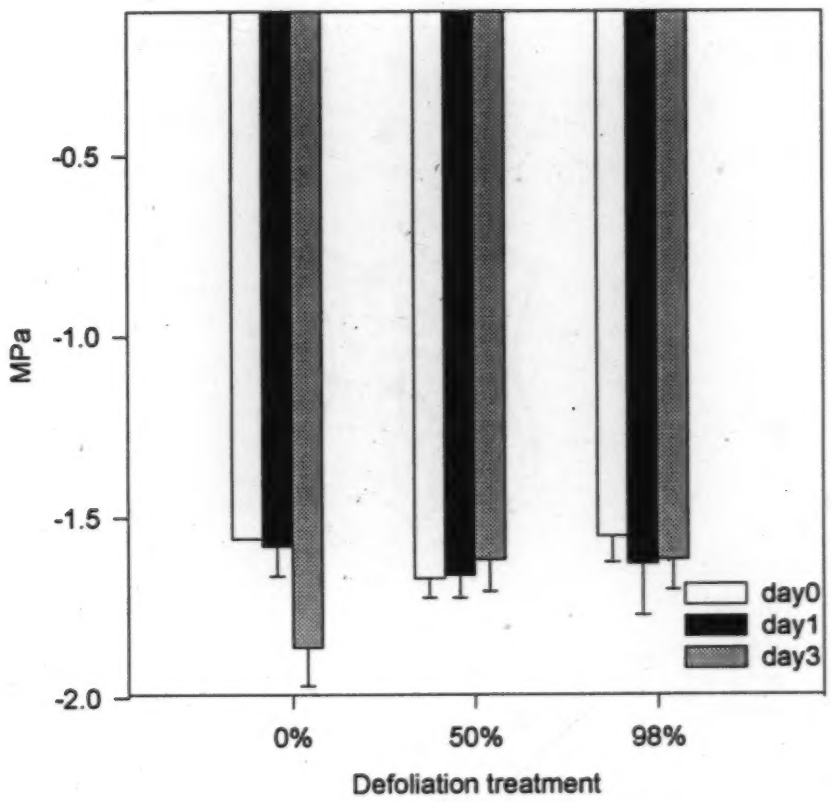

Figure 3: Pre- and post-defoliation leaf water potential for three defoliation levels measured in the field, at Ellerslie.

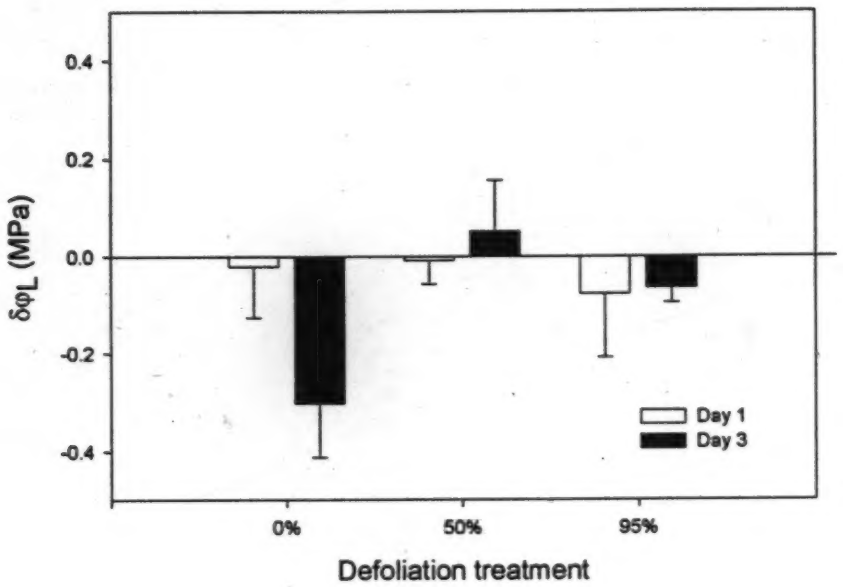

Figure 4: Change in leaf water potential from pre-defoliation for three defoliation levels, Ellerslie.

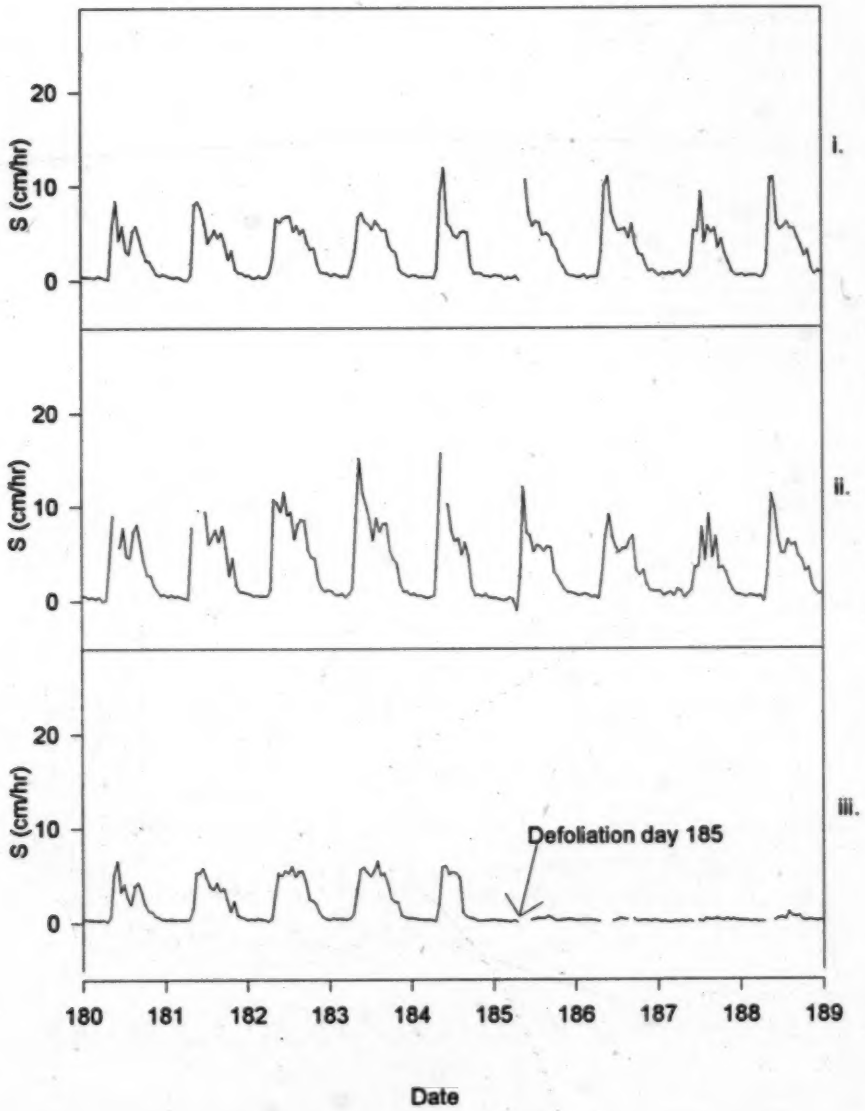

Figure 5a: Typical tree-level sap flow velocity for clone from Botanical Gardens. i: 0% defoliation ii: 50% defoliation iii: 98% defoliation.

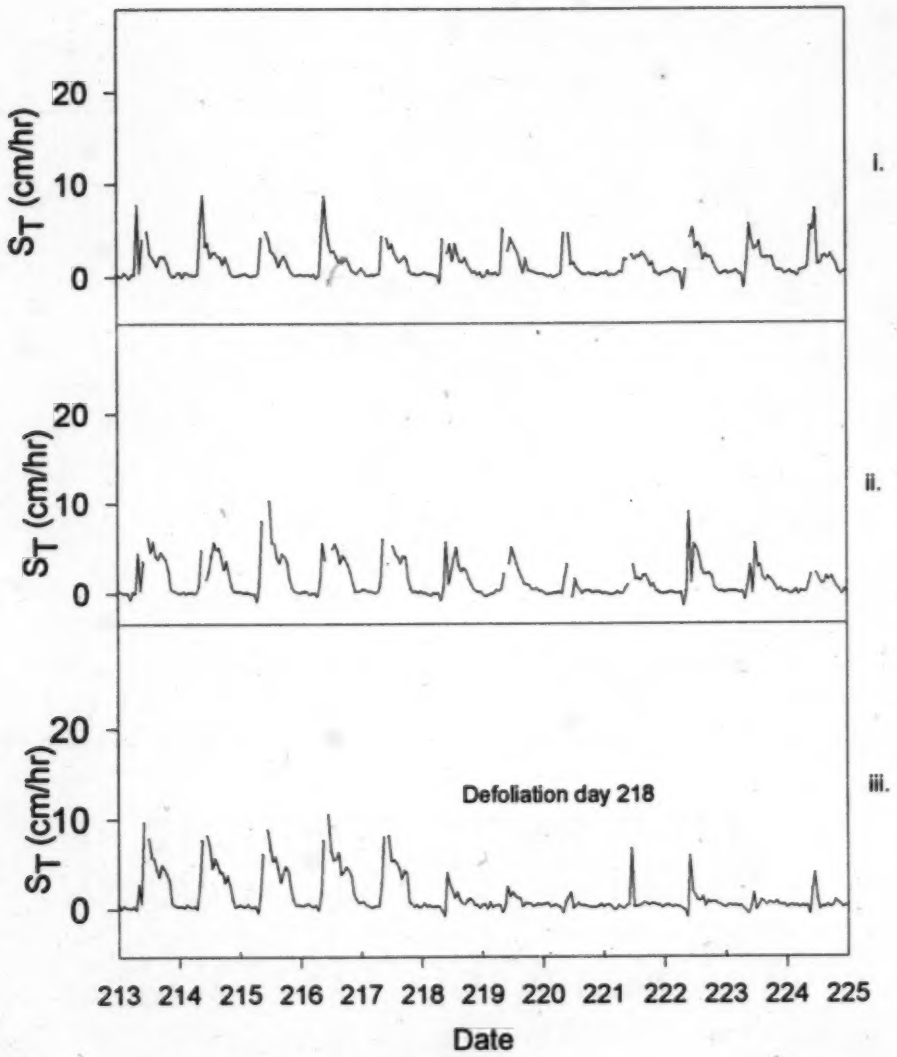

Figure 5b: Typical tree-level sap flow velocity for clone from Woodbend 2 i. 0% defoliation, ii. 50% defoliation, iii. 98 % defoliation

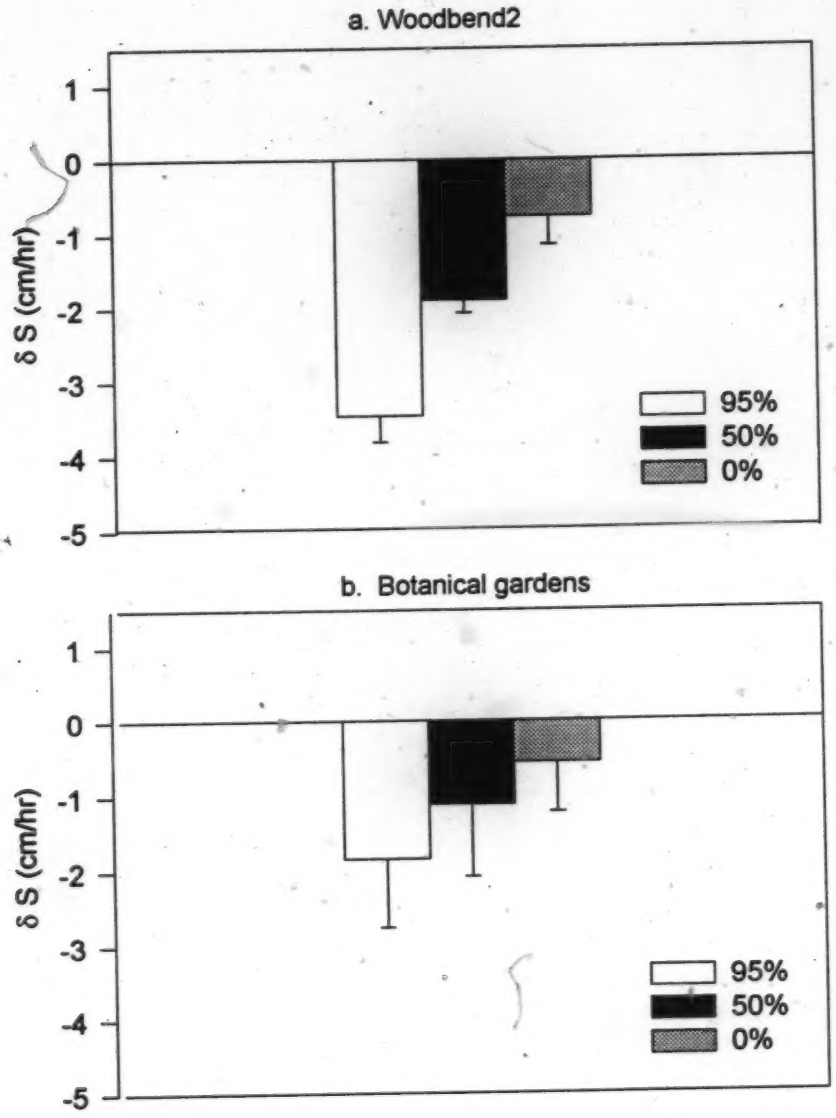

Figure 6: Changes in tree-level sap flow velocity from pre-defoliation for three defoliation levels: a. Woodbend2 b. Botanical Gardens.

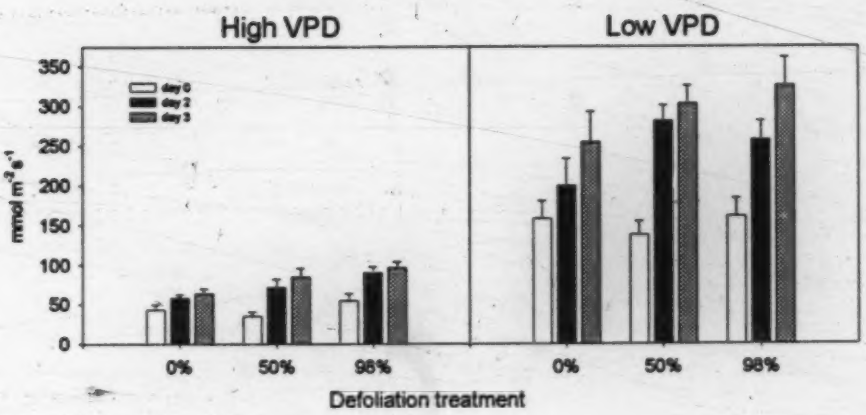

Figure 7: Pre- and post-defoliation stomatal conductance data for three defoliation and two VPD (1.9kPa and 0.64 kPa) treatments under controlled environmental conditions.

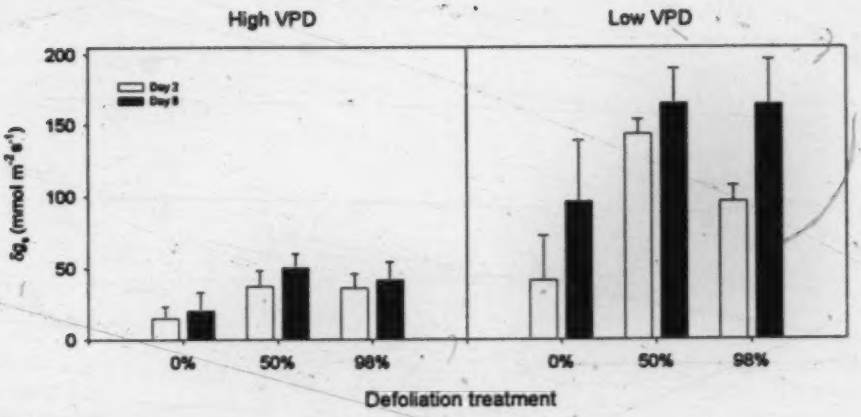

Figure 8: Change in stomatal conductance from pre-defoliation for three defoliation and two VPD (1.9kPa and 0.64 kPa) treatments under controlled environmental conditions.

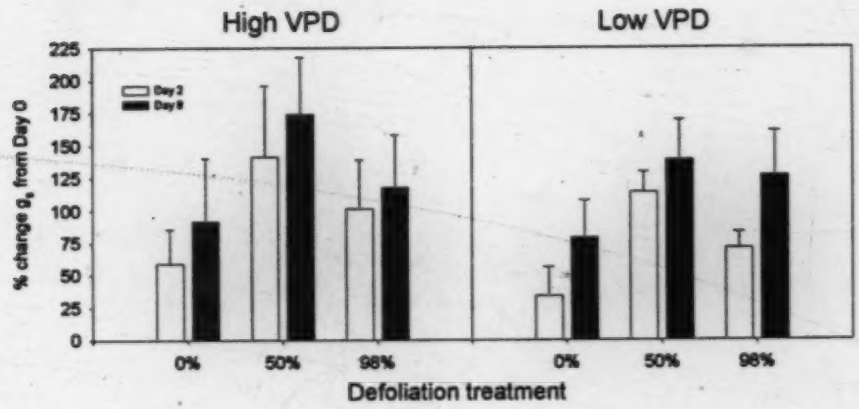

Figure 9: Relative change in stomatal conductance from pre-defoliation for three defoliation and two VPD (1.9kPa and 0.64kPa) treatments under controlled environmental conditions.

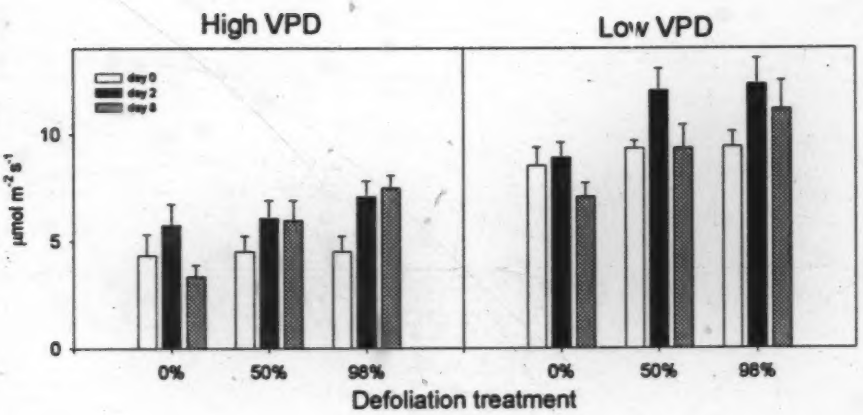

Figure 10: Pre- and post-defoliation $C0_2$ assimilation data for three defoliation and two VPD (1.9kPa and 0.64 kPa) treatments under controlled environmental conditions.

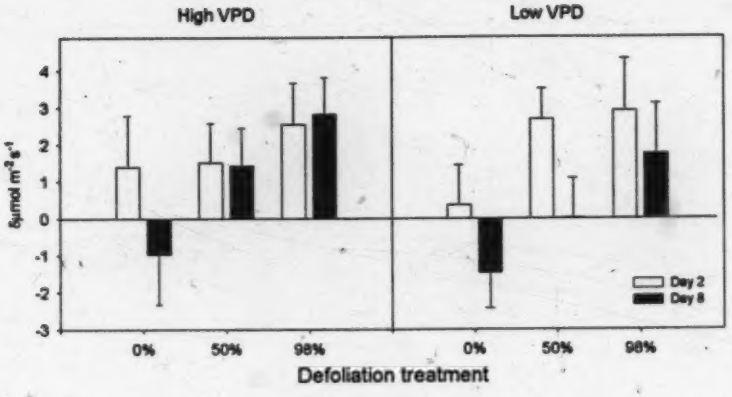

Figure 11: Changes in $C0_2$ assimilation from pre-defoliation for three defoliation and two VPD (1.9kPa and 0.64kPa) treatments under controlled environmental conditions.

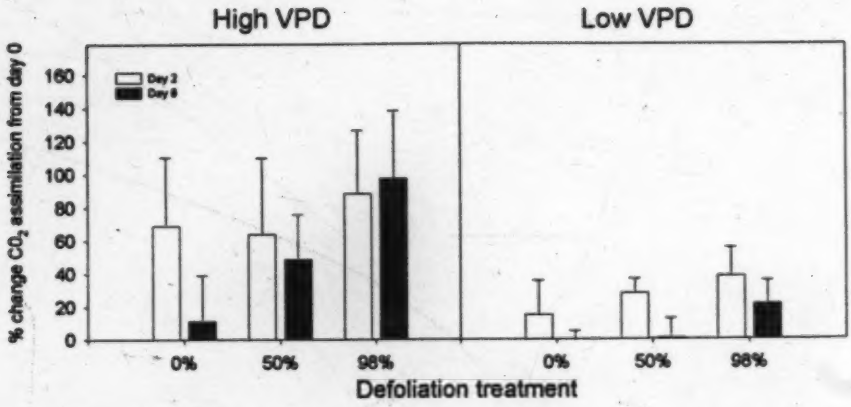

Figure 12: Relative change in $C0_2$ assimilation from pre-defoliation for three defoliation and two VPD (1.9kPa and 0.64 kPa) treatments under controlled environmental conditions.

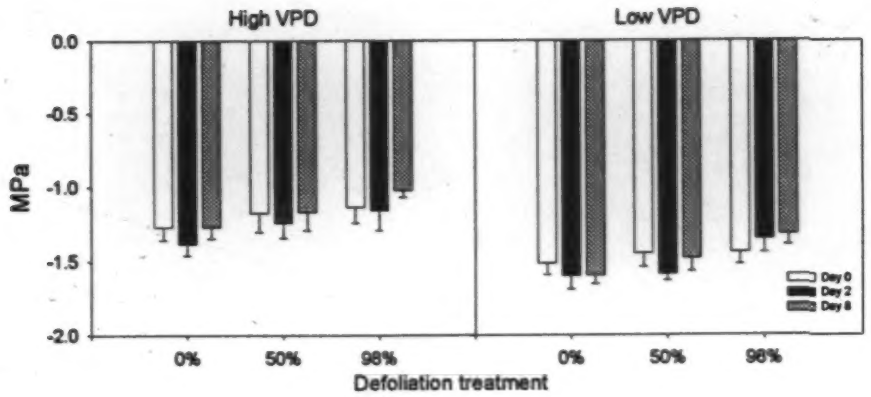

Figure 13: Pre- and post-defoliation leaf water potential data for three defoliation and two VPD (1.9kPa and 0.64 kPa) treatments under controlled environmental conditions.

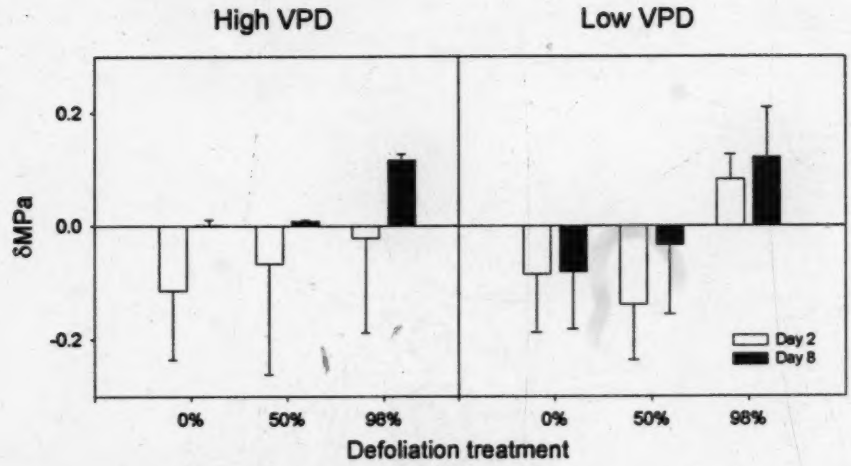

Figure 14: Changes in leaf water potential from pre-defoliation measurements for three defoliation and two VPD (1.9kPa and 0.64kPa) treatments under controlled environmental conditions.

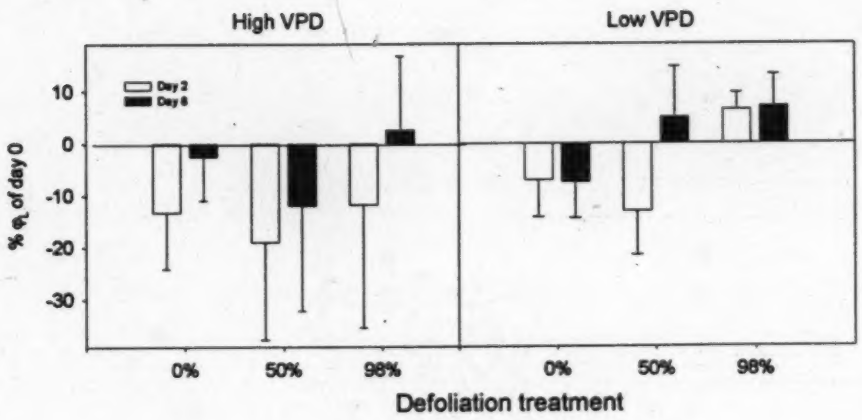

Figure 15: Relative change in leaf water potential from pre-defoliation for three defoliation and two VPD (1.9kPa and 0.64 kPa) treatments under controlled environmental conditions.

	Sap flow (cm/hr) ± S.E.					
	95% defoliation		50% defoliation		0% defoliation	
Site/Clone	PRE	POST	PRE	POST	PRE	POST
WB2-J	5.9 ±0.7	2.6±0.2	6.1±0.2	4.7±0.2	4.0±0.1	2.8±0.2
WB2-K	4.9±0.4	2.1±0.2	6.0±0.5	4.1±0.1	.	.
WB2-M	5.6±0.7	1.5±0.1	5.6±0.4	3.3±0.3	4.1±0.1	3.9±0.2
BG-A	2.4±0.2	0.4±0.1	3.5±0.4	1.8±0.6	5.9±0.4	5.6±0.5
BG-B	4.3±0.4	1.7±0.2	3.5±0.3	1.9±0.1	5.5±0.4	5.1±0.7
BG-C	2.1±0.2	0.5±0.1	4.9±0.4	3.9±0.3	1.5±0.2	1.4±0.1
BG-D	4.8±0.3	0.7±0.1	9.9±0.5	7.8±1.0	5.6±0.2	7.3±1.2

Appendix 1: Average daily sap flow pre- and post-defoliation for sites Woodbend2 (WB2) and Botanical Gardens (BG).

Source	df	ANOVA SS	Mean Square	F	p
Clone	5	0.083	0.017	2.87	0.53
Defoliation	2	0.49	0.25	42.67	0.0017
Clone*Defoliation	10	0.19	0.019	3.30	0.019
Time	1	0.0040	0.040	0.70	0.42
Defoliation*Time	2	0.014	0.014	1.17	0.34

*error term for Clone and Defoliation is Clone*Defoliation, for all other terms it is Clone*Defoliation*Time

Appendix 2: Split-plot ANOVA for stomatal conductance measurements at Ellerslie.

Source	df	ANOVA SS	Mean Square	F	p
Clone	5	57.68	11.54	2.08	0.15
Defoliation	2	21.87	10.94	1.98	0.19
Clone*Defoliation	10	55.33	5.53	1.62	0.19
Time	1	5.14	5.14	1.51	0.23
Defoliation*Time	2	19.27	9.63	2.83	0.09

*error term for Clone and Defoliation is Clone*Defoliation, for all other terms it is Clone*Defoliation*Time

Appendix 3: Split-plot ANOVA for leaf water potential measurements at Ellerslie.

Source	df	ANOVA SS	Mean Square	F	p
Clone	6	7.07	1.18	0.72	0.64
Defoliation	2	10.92	5.46	3.34	0.07

*Error term is Clone*Defoliation

Appendix 4: RCB ANOVA for sap flow measurements at Woodbend 2 and Ellerslie.

Source	df	ANOVA SS	Mean Square	F	p
Defoliation	2	53644.05	26822.02	6.24	0.0042
VPD*Defoliation	2	25357.41	12678.70	2.95	0.063
Tree(VPD*Defoliation)	42	180414.64	4295.59	1.17	0.30
Time	1	32.67	32.67	0.01	0.93
VPD*Time	1	1209.50	1209.50	0.33	0.57
Defoliation*Time	2	14155.54	7077.77	1.94	0.16
VPD*Defoliation*Time	2	2219.97	1109.98	0.30	0.74

*Error term for Defoliation and VPD*Defoliation is Tree(VPD*Defoliation), for all other terms it is VPD*Defoliation*Time

Appendix 5: Split plot, 2-way ANOVA for difference of stomatal conductance measurements under controlled environmental conditions.

Source	df	ANOVA SS	Mean Square	F	p
Defoliation	2	41.95	20.98	1.75	0.92
VPD*Defoliation	2	5.84	2.92	0.24	0.78
Tree(VPD*Defoliation)	42	503.26	11.98	0.95	0.57
Time	1	11.41	11.41	0.90	0.35
VPD*Time	1	38.68	38.68	3.05	0.09
Defoliation*Time	2	17.32	8.66	0.68	0.51
VPD*Defoliation*Time	2	24.99	12.50	0.99	0.38

*Error term for Defoliation and VPD*Defoliation is Tree(VPD*Defoliation), for all other terms it is VPD*Defoliation*Time

Appendix 6: Split plot, 2-way ANOVA for difference of leaf water potential measurements under controlled environmental conditions.

Source	df	ANOVA SS	Mean Square	F	p
Defoliation	2	113.39	56.70	4.13	0.02
VPD*Defoliation	2	14.07	7.04	0.51	0.60
Tree(VPD*Defoliation)	42	575.93	13.71	2.01	0.01
Time	1	43.88	43.88	6.44	0.02
VPD*Time	1	1.21	1.21	0.18	0.68
Defoliation*Time	2	8.78	4.39	0.64	0.53
VPD*Defoliation*Time	2	21.89	10.94	1.60	0.21

*Error term for Defoliation and VPD*Defoliation is Tree(VPD*Defoliation), for all other terms it is VPD*Defoliation*Time

Appendix 7: Split plot, 2-way ANOVA for difference of $C0_2$ assimilation measurements under controlled environmental conditions.

Source	df	ANOVA SS	Mean Square	F	p
Defoliation	2	93063.66	46531.83	2.85	0.069
VPD*Defoliation	2	1636.69	818.34	0.05	0.95
Tree(VPD*Defoliation)	42	685535.65	16322.28	4.74	0.0001
Time	1	28686.88	28686.88	8.33	0.0061
VPD*Time	1	1272.40	1272.40	0.37	0.55
Defoliation*Time	2	473.95	236.98	0.07	0.93
VPD*Defoliation*Time	2	2242.69	1211.35	0.33	0.72

*Error term for Defoliation and VPD*Defoliation is Tree(VPD*Defoliation), for all other terms it is VPD*Defoliation*Time

Appendix 8: Split plot, 2-way ANOVA for % of day 0 stomatal conductance measurements under controlled environmental conditions.

Source	df	ANOVA SS	Mean Square	F	p
Defoliation	2	2947.10	1473.55	0.59	0.56
VPD*Defoliation	2	449.19	224.59	0.09	0.91
Tree(VPD*Defoliation)	42	104047.12	2477.31	10.61	0.0001
Time	1	1058.01	1058.02	4.53	0.04
VPD*Time	1	394.88	394.88	1.69	0.20
Defoliation*Time	2	26.28	13.14	0.06	0.95
VPD*Defoliation*Time	2	222.68	111.34	0.48	0.62

*Error term for Defoliation and VPD*Defoliation is Tree(VPD*Defoliation), for all other terms it is VPD*Defoliation*Time

Appendix 9: Split plot, 2-way ANOVA for % of day 0 leaf water potential measurements under controlled environmental conditions.

Source	df	ANOVA SS	Mean Square	F	p
Defoliation	2	24613.24	12306.62	1.23	0.30
VPD*Defoliation	2	3902.68	1951.34	0.19	0.82
Tree(VPD*Defoliation)	42	420579.42	10013.80	3.63	0.0001
Time	1	13220.32	13220.32	4.80	0.03
VPD*Time	1	0	0	0	1.00
Defoliation*Time	2	4380.53	2190.26	0.79	0.46
VPD*Defoliation*Time	2	4146.92	2073.46	0.75	0.48

*Error term for Defoliation and VPD*Defoliation is Tree(VPD*Defoliation), for all other terms it is VPD*Defoliation*Time

Appendix 10: Split plot, 2-way ANOVA for % of day 0 $C0_2$ assimilation measurements under controlled environmental conditions.

Source	df	ANOVA SS	Mean Square	F	p
Defoliation	2	228.59	114.30	24.1	0.04
VPD*Defoliation	2	9.49	4.74	0.36	0.70
Time	2	92.52	46.26	3.49	0.033
Defoliation*Time	4	159.91	39.98	3.02	0.02

*Error term for Defoliation is VPD*Defoliation, for all other terms it is VPD*Defoliation*Time

Appendix 11: 2-way ANOVA for pre- and post-defoliation stomatal conductance measurements under controlled environmental conditions.

Source	df	ANOVA SS	Mean Square	F.	p
Defoliation	2	99.97	49.99	52.38	0.019
VPD*Defoliation	2	1.91	0.95	0.15	0.86
Time	2	15.57	7.79	1.23	0.30
Defoliation*Time	4	14.41	3.60	0.57	0.69

*Error term for Defoliation is VPD*Defoliation, for all other terms it is VPD*Defoliation*Time

Appendix 12: 2-way ANOVA for pre- and post-defoliation leaf water potential measurements under controlled environmental conditions.

Source	df	ANOVA SS	Mean Square	F	p
Defoliation	2	29740.64	14870.32	6.34	0.14
VPD*Defoliation	2	4687.39	2343.70	0.65	0.53
Time	2	202254.54	101127.27	27.88	0.0001
Defoliation*Time	4	19467.54	4866.89	1.34	0.26

*Error term for Defoliation is VPD*Defoliation, for all other terms it is VPD*Defoliation*Time

Appendix 13: 2-way ANOVA for pre- and post-defoliation $C0_2$ assimilation measurements under controlled environmental conditions.

	g_s (mmol m^{-2} s^{-1}) ± S.E.		
Defoliation Treatment	Pre-defoliation	Day 1 Post	Day 3 Post
0%	326 ± 13	343 ± 11	314 ± 18
50%	316 ± 21	400 ± 22	405 ± 18
98%	313 ± 17	418 ± 13	418 ± 24

Appendix 14: Mean pre- and post-defoliation stomatal conductance values for three defoliation treatments over three measurement days at Ellerslie.

	φ_{leaf} (MPa) ± S.E.		
Defoliation Treatment	Pre-defoliation	Day 1 Post	Day 3 Post
0%	-1.56 ± 0.07	-1.58± 0.08	-1.86± 0.11
50%	-1.67 ± 0.06	-1.66± 0.06	-1.62± 0.09
98%	-1.55 ± 0.07	-1.63± 0.14	-1.62± 0.08

Appendix 15: Mean pre- and post-defoliation leaf water potential values for three defoliation treatments over three measurement days at Ellerslie.

	g_s (mmol m^{-2} s^{-1}) ± S.E.					
	Pre-defoliation		Day 2 Post		Day 8 Post	
Defoliation Treatment	High VPD	Low VPD	High VPD	Low VPD	High VPD	Low VPD
0%	44±6.7	158±23	58±4.0	200 ±34	64 ±6.6	255 ±38
50%	35±5.4	138±17	72±10	282 ±19	85 ±11	303 ±23
98%	55±9.1	161±23	91±6.9	258 ±24	96 ±7.6	225 ±36

Appendix 16: Mean pre- and post-defoliation stomatal conductance values for three defoliation and two VPD (1.9kPa and 0.64kPa) treatments under controlled environmental conditions.

	φ_{leaf} (MPa) ± S.E.					
	Pre-defoliation		Day 2 Post		Day 8 Post	
Defoliation Treatment	High VPD	Low VPD	High VPD	Low VPD	High VPD	Low VPD
0%	-1.27±0.09	-1.51±0.08	-1.38±0.07	-1.60±0.09	-1.27±0.08	-1.59±0.06
50%	-1.17±0.13	-1.45±0.09	-1.24±0.10	-1.58±0.09	-1.16±0.12	-1.48±0.09
98%	-1.13±0.11	-1.44±0.08	-1.15±0.14	-1.35±0.09	-1.01±0.05	-1.31±0.07

Appendix 17: Mean pre- and post-defoliation leaf water potential values for three defoliation and two VPD (1.9kPa and 0.64kPa) treatments under controlled environmental conditions.

	$C0_2$ assimilation ($\mu mol\ m^{-2}\ s^{-1}$) ± S.E.					
	Pre-defoliation		Day 2 Post		Day 8 Post	
Defoliation Treatment	High VPD	Low VPD	High VPD	Low VPD	High VPD	Low VPD
0%	4.3±1.0	8.5±0.9	5.7±1.0	8.9±0.7	3.4±0.5	7.1±0.7
50%	4.5±0.7	9.3±0.4	6.1±0.8	12.0 ±1.0	6.0±1.0	9.3±1.1
98%	4.5±0.7	9.4±0.7	7.1±0.7	12.3 ±1.2	7.5±0.5	11.2±1.4

Appendix 18: Mean pre- and post-defoliation $C0_2$ assimilation values for three defoliation and two VPD (1.9kPa and 0.64kPa) treatments under controlled environmental conditions.

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